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THE BOTANICAL REVIEW

Interpreting Botanical Progress

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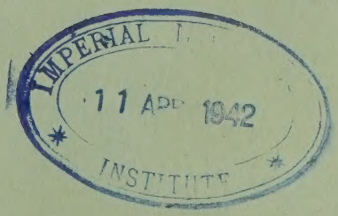

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ERRATA

Certain egregious errors concerned chiefly with citations to the literature in Part I and Part II of this paper should be corrected as follows:

Part I

Page	4,	line	22—	change	(382)	to (332)
"	4,	"	27—	"	(64)	to (62)
"	6,	"	35—	"	(62)	to (64)
"	8,	"	27—	"	(308)	to (307)
"	8,	"	29—	"	(191)	to (291)
"	12,	"	39—	"	(276)	to (382)
"	12,	"	39—	"	(137)	to (136)
"	15,	"	25—	"	(324)	to (349)
"	16,	"	30—	"	(303)	to (302)
"	18,	"	19—	"	(410)	to (481)
"	20,	"	9—	"	(339)	to (341)
"	23,	"	38—	"	(409)	to (436)
"	25,	"	27—	"	(234)	to (254)
"	26,	"	30—	omit	(410)	
"	32,	"	10—	change	(493)	to (527)
"	39,	"	22—	"	(134)	to (139)
"	39,	"	24—	"	(339)	to (340)
"	41,	"	26—	"	(388)	to (393)
"	43,	"	24—	omit	(cytochrome)	
"	47,	"	5—	change	(64)	to (62)
"	47,	"	9—	"	(64)	to (63)

Part II

Page	108,	line	22—	change	(506) to (577)
"	108,	"	26—	omit	((*cf.* 506))
"	110,	"	3—	change	(331) to (329)
"	110,	"	7—	"	(528) to (525)
"	110,	"	20—	"	(tropistic) to (tropic)
"	111,	"	10—	"	(hold) to (holds)
"	114,	"	17—	after	(Popp) insert ((400))
"	114,	"	37—	change	(344) to (345)
"	118,	"	8—	after	(Ray) insert (in)
"	118,	"	9—	change	((1686)) to (1686); after (Linnaeus) insert (in); change ((1732)) to (1732)
"	126,	line	17—	change	(441) to (414)
"	127,	"	38—	"	(223) to (416)
"	128,	"	33—	"	(198) to (98)
"	129,	"	31—	"	(414) to (408)
"	140,	"	14—	"	(Chialakhian) to (Chailakhian)
"	144,	"	25—	"	(135, 508) to (146, 543)
"	148,	"	22—	"	(91- . 1918.) to (89-204. 1919)
"	168,	"	49—	after	(1935.) insert ((See also: Jour. Amer. Med. Assoc. 93 (2): 1868–1874. 1929.))

THE BOTANICAL REVIEW

VOL. II MARCH, 1936 NO. 3

THE RÔLE OF LIGHT IN THE LIFE OF PLANTS

II. THE INFLUENCE OF LIGHT UPON GROWTH AND DIFFERENTIATION

PAUL R. BURKHOLDER

Department of Botany, Connecticut College

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GROWTH

The relation of light to the physical and chemical constitution of plants, as discussed in the first part, would lead one to expect a profound influence upon growth and production of morphological characters. Preliminary to further discussion concerning the action of light upon processes involved in *growth* and *differentiation,* it may be well to define what is meant by these terms.

Growth may be defined as irreversible increase in the size of an organism or its parts as a result of the incorporation of materials from the environment; new protoplasm is synthesized, cellular boundaries are extended and weight is increased. The final results of the integrated processes of growth may be measured in terms of weight, volume, length, number, etc. Growth may be accomplished in one or both of two different ways: (a) cell multiplication and limited cell enlargement and (b) cell enlargement which is unlimited within a comparatively wide range. In order to dis-

tinguish clearly between these two methods of growth (*cf.* 231) the term *meresis* has been proposed to signify increase in cell number by meristematic activity, promoted perhaps through the agency of "meristins" (263) or "biotin" (247); and the name *auxesis* has been applied to growth by continued cell enlargement, activated by growth-substances or "auxins" (247). Increase in size by repeated cell divisions necessitates synthesis of new protoplasm and, in consequence, there results a gain in dry weight by the accumulation of carbohydrates, fats, proteins, etc. Following cell divisions, considerable increase in volume may be accomplished through further cell enlargement brought about by the processes of hydration, vacuolation, or extensive polarized growth, which need not be accompanied necessarily by appreciable increment in solid matter. The metabolic processes leading to formation of new protoplasm and new cells are conditioned mainly by the supply of organic nutrients to growing centers or meristems. The more obvious manifestations of growth by cell enlargement are concerned chiefly with absorption of water and plastic extension of the cell walls. Increasing hydration is usually accompanied by vacuolation, and frequently by changes in the composition of the wall, so that this phase of growth may be looked upon also as a step in the direction of differentiation. In view of the studies made by Priestley (410), Schuepp (478), and others, it appears that even the vacuolated type of cell may synthesize protoplasm and undergo divisions, thus contributing to growth through increase in cell number as well as in cell size. The production of form and structure in plants will be discussed later under the heading *differentiation.*

LIGHT AND DARKNESS

It has been emphasized by recent workers that light is important for meristematic activity in green plants through photosynthesis of organic foods, absorption of mineral matter, and regulation of the water supply. If other conditions are favorable, photosynthesis should proceed unchecked in continuous light and the food available for growth might be expected to vary with the exposure period. It has been found, however, that the length of the daily light period not only affects the quantity of material formed, but also influences the use which the plant can make of it. In those plants which store food in tubers, vegetative growth is best in long

daily light exposure periods. In somewhat shorter periods these same plants store carbohydrates, but in very short periods the total light energy becomes a limiting factor in CO_2 assimilation. In bulb-forming plants, like the onion, growth is favored in days shorter than the optimum for food storage (146). There appears to be an optimal light/darkness ratio for the maximum utilization of organic materials for stem growth. Light seems to exert a "regulatory action on the internal processes of the plant other than those which merely determine the total quantity of carbohydrate produced," and it has been suggested that this regulation by light may be concerned with internal water supply, *i.e.*, the degree of hydration of the living cell contents (146).

The action of visible radiation upon growing organs is striking when comparisons are made between the rates of enlargement in darkness and in light of different intensity values. From the time of DeCandolle (*cf.* 373) and of Sachs (452) many instances are on record to show that growth fluctuates greatly during the natural alternation of day and night. Thus, bamboo grows more rapidly at night provided the temperature permits a just comparison (403, *cf.* 320), and corn behaves in like manner (183). The same behavior has been reported by Mason (303) for the date palm whose organs cease elongation in full sunlight but resume growth slowly in diffused light and rapidly at night. Growth of the palm leaves was apparently correlated with closing of the stomata, checking of transpiration and increased turgesence in the meristematic tissues.

Brown and Trelease (59) found that shoots of *Cestrum nocturnum* decreased in length due to water loss by transpiration during the day but recovered their original size later in the afternoon and increased in length by rapid growth at night. Trelease (549) observed a more rapid rate of elongation in banana leaves at night associated with greater turgidity as compared with conditions in the daytime.

In some plants, such as succulent cacti, the rate of growth during day and night varies according to the acidity of the tissues. In the daylight, greater growth of *Opuntia* sp. appears to be synchronous with decreased acidity, while at night or in dim light there is a lessened growth rate along with accumulation of acids (*cf.* 544). Popp (401) grew soy beans under controlled conditions in a series

of light intensities ranging from 26 to 4285 f. c. and observed that the lower the light intensity the more rapid was the rate of stem elongation during the period of initial growth. Reid (436) observed that illuminated seedlings grown in an atmosphere lacking in CO_2 were shorter and weighed less than similar seedlings grown in darkness. However, seedlings grown in light (minus CO_2) had larger leaves and cotyledons than those grown in darkness.

The remarkable and abnormal differences in the form, structure and color of plants grown in continuous darkness have been observed and described so frequently that the term "etiolation" has come to have a well-known significance. From the present viewpoint, the great increase in length of the shoot axis in darkness is particularly interesting in those instances where an ample supply of food for growth is available in the storage reserves of seeds, tubers, rhizomes, etc. When such plants are grown in darkness, the internodes are long, the leaves fail to expand and are devoid of chlorophyll, and the root system is poorly developed. According to Figdor (125), etiolated shoots of *Bowiea volubilis* have elongated internodes in the main axis, and branching is very much reduced.

Andrews (6) reported that *Vicia faba,* growing in the light, reached a stem height of 5 cm. and a diameter of 7 mm. in 12 days, but in the dark a height of 30 cm. and a diameter of $\pm$ .75 mm. was attained in the same time. Overbeek (374) reported a growth retardation of over 50 per cent in illuminated *Raphanus* seedlings as compared with control plants kept in darkness. Skutch (501) found that the leaf sheaths of banana became abnormally elongated when placed in darkness for some time. Priestley and Ewing (413) and Priestley (407) have described the structure and morphological responses exhibited by growing seedlings of *Vicia* and *Pisum* when in total darkness and in a series of daily light exposures varying from one minute up to several hours. Light exposures tended to remove the symptoms of etiolation by shortening the internodes, expanding the leaf laminae and causing chlorophyll formation. Trumpf (550) carried out some novel experiments to test the effect of daily exposures to light of different colors upon the growth of *Phaseolus multiflorus.* Using an arc lamp and short exposures of 1, 5, 10 and 30 minutes it was possible to obtain plants which tended to appear more nearly normal

in size and form without development of chlorophyll. Blue rays prevented stem elongation more than did red wave lengths of light. Similar evidence has been obtained by Teodoresco (533) and Funke (138), both of whom grew many kinds of plants with available stored food under different colored glass filters. Blue radiation seemed to cause short petioles and short internodes, while red light, acting in a manner similar to darkness, permitted their excessive elongation. Lange (264) has demonstrated that exposure of germinating *Avena* seed to bright daylight during the period of swelling inhibits any appreciable elongation of the first internode ("mesocotyl") in the seedling. Even exposure to phototropically inactive red light during the swelling period, and for 12–16 hours after emergence of the coleoptile, almost completely inhibited elongation of the first internode. Boysen-Jensen (51) and others have observed how the coleoptile of *Avena* elongates more in darkness than in light. Hamada (181) found that the effect of light upon growth of the *Avena* seedling varied with its age. The first internode was stunted by light, while growth of the primary leaf was stimulated.

Coupin (85) carried out some interesting experiments with *Lupinus* seedlings grown in light and in darkness. Extracts from the light grown plants, when applied to the nutrient solution of seedlings kept in darkness, prevented excessive elongation of the internodes so characteristic of ordinary etiolated plants. Coupin concluded that the action of light on the chloroplasts caused the formation of some substance which prevented etiolation. Trumpf (551) repeated these experiments with *Phaseolus* seedlings and found that the sugar in the expressed sap was responsible for the effects observed on stem elongation, and that the sap of both light and dark grown plants hindered growth of seedlings in darkness when the expressed juice was added to the cultures.

The effects of light and darkness upon growth and development of plants may be summarized briefly as follows: In the complete absence of light, plants with available stored food become etiolated. If a little light is available, the extreme symptoms of etiolation are modified, *i.e.*, the leaves unfold and develop chlorophyll, and the internodes tend to grow somewhat shorter. With further increase in light intensity up to about 20 to 50 per cent of ordinary daylight, the size of the leaves and height of the plant attain a maximum.

Exposure to full sunlight brings about a slight decrease in height, in length of internode and in area of leaves, but these effects are associated with an increase in percentage of dry weight, in number of branches, in size of roots, and frequently also in flowers and fruit (*cf.* 492).

CELL MULTIPLICATION

In considering the fundamental nature of the light- and dark-growth phenomena recorded in the literature, it is very difficult to conclude whether observed increases in size may have resulted from increases in the number, or in the size of the constituent cells, or both. In too few instances have determinations been made concerning the behavior of the cells in growing organs, but it seems fairly certain that meristematic activity probably plays a greater part in the phenomenon of increased organ stretching under reduced light conditions (as already described) than is generally believed. Etiolation experiments, designed to compare relative growth and development in darkness and in light, have been conducted usually with growing tubers, seeds, spores, etc., which possess an abundance of food. Since the food supply is of proportionately greater importance for the processes of cell multiplication than for the enlargement of cells through increased hydrolysis, the nutritive factor must be taken into account for the correct interpretation of data given in light-growth experiments.

Interesting facts concerning cell multiplication have been derived from the growth behavior of unicellular green algae. It has been found in *Scenedesmus costulatus* (56), growing in a mineral salts solution, that the rate of increase in growth is approximately proportional to the rate of increase in light intensity until a certain optimum illumination is reached. In experimental cultures grown under different intensities of light covering a considerable range, the addition of glucose to the culture medium did not increase the growth rate beyond that normally found under autotrophic conditions associated with optimal light intensities. When glucose was supplied in the complete absence of light, the shape of the growth line was much less steep than under the conditions of optimal autotrophism in inorganic solutions or partial saprophytism in glucose solutions in the light. Increased light intensity has been reported to shorten the intervals of time between cell divisions

(135), in developing zoospores of *Oedogonium pluviale*. An accelerating effect upon protoplasmic synthesis through carbohydrate supply has been suggested to account for this increased division rate.

Several investigators have found a periodicity in the occurrence of cell division in root tips. The results, though not entirely in agreement, indicate that there are often about two division maxima during a 24 hour period, one of which occurs about midday (*cf.* 488). Diffuse light has been reported as favorable to continued growth of excised root tips in nutrient culture (439). Drooglever (107) has observed rhythmical division in *Allium* with an alternating maximum and minimum in constant darkness. Illumination during the daytime changed the rhythm to a diurnal period with the largest number of divisions taking place in darkness. Some possible relation of light to nuclear processes has been suggested by the optical sensitization of root tips with dilute dyes (406) whereby abnormal mitoses and retarded growth were obtained (*cf.* 328). Satisfactory information concerning the effects of light and other factors upon mitosis is indeed meagre.

In considering the action of light upon growth in lower organisms, a recent report from the field of bacteriology is of interest. Fraps and Sterges (134) determined the rates of oxidation of three different salts of ammonia in six soil types, and found that while 41 per cent of the ammonia was oxidized in darkness, only 5 per cent was changed in sunlight during the same time. Apparently, sunlight was injurious to the growth of the nitrifying organisms. Recent work by Meier (315) has indicated that multiplication of the unicellular green alga, *Stichococcus bacillaris,* is proportional to the intensity of illumination ranging from 3.76 to 34.1 microwatts/mm^2. A higher intensity such as 102.0 microwatts/mm^2 checked the growth of this alga. Some portions of the spectrum were not favorable but a wide complex of wave lengths from 0.6 to 1.4 microns was moderately effective in promoting multiplication of the algae. The cell multiplication of diatoms is reported also as being dependent upon the energy of the incident radiation, probably due to the nutritive relationships (517). Cell multiplication in *Volvox* and *Closterium* has been found to be greater in red than in blue light, (242) probably also because of

the relative efficiency for CO_2 assimilation. Experiments by Teodoresco (533) and others concerning the number and size of cells in the thalloid bodies of cryptogams grown in the light and darkness have given striking results. When spores were germinated in blue or white light, the number of cells in the sporeling was greater than when grown in red light or in darkness. In regard to the effect of light upon bacteria, it may be said that visible light acting for a long time has an inhibiting effect upon their multiplication, while ultra-violet radiation exerts a lethal action dependent upon its absorption and energy (599).

In multicellular higher green plants, it is more difficult to evaluate the effect of light upon growth by cell number due to mutual contact and pressure of the cell units one upon the other. The peculiar etiolation effects obtained when herbaceous plants are grown in darkness have been explained by Priestley on the basis of the availability of soluble foods to the meristematic tissues. Due to the superficial position of the apical shoot meristem, any variation in its food and water supply would certainly be reflected in its growth behavior (383). The size and number of epidermal cells were determined in etiolated and normal plants of *Phaseolus multiflorus* by Brotherton and Bartlett (58). Increase in length of the etiolated stem was estimated as due 34% to increased cell divisions and the other 66% was accounted for by increase in length of the constitutent cells. Penfound (386), who grew *Helianthus* under different conditions of light and soil moisture, found that the increased height of shade-grown plants was due to an increase in the number of cells, not increase in length of cells, along the vertical axis. The repressing effect of light upon sprouting in potato tubers stored either in daylight or in artificial light has been shown to be very marked as compared with controls kept in darkness (574).

In the growth of storage organs, seeds and vegetative parts of the plant body, light appears to play an important rôle through the processes of nutrition and hydration and perhaps photocatalysis. Whether light plays any important part in the production and activity of substances which have been considered by certain investigators to be specific for cell divisions such as glutathione (182), Wuchsstoff B (4), biotin (247) and bios (324), is not known.

CELL ENLARGEMENT

The effect of light upon the enlargement of organs and tissues has been shown by several different investigators to be concerned, to a considerable extent, with growth of the individual cell-components. Long ago, Kraus (255) investigated the matter of cell size and number in etiolated and normal leaves and stems of several species of plants. The epidermal cells of etiolated internodes were nearly always longer than those in normal plants, and sometimes an increase in cell length was accompanied also by increase in the number of cells. The characteristic elongation of stems in darkness appears to be the result chiefly of a considerable increase in the mean length of the component cells. Redington (430) found that long light exposure resulted in decreased cell formation and cell elongation in the stems of *Kleinia* and *Linum*. The growth period and final size of leaves were greater in 16 hours of light and 8 hours of dark per day than in continuous light. In 8 hours of light alternating with 16 hours of darkness there resulted very long petioles and small laminae. Measurements of endodermal cell length in the stems of flax, hemp, hop, salvia, hibiscus and cotton indicated that the linear dimension varied inversely with the light period (429). Doroshenko (104) reported a reduction in cell-size of wheat, barley and flax when subjected to a moderately short day; however, further decrease in the daily light exposure brought about an increase in length of the cells. On the other hand, Jeffs (224) found no effect of light upon the elongation of root hairs in *Raphanus sativus* or in *Sinapis alba*.

Küster (260) has shown that the cells of etiolated shoots are larger and less differentiated than those of normal light growing plants. Brotherton and Bartlett (58), as has already been mentioned, reported that about two-thirds of the increased length of the etiolated stem may be due to increase in cell length. Klebs (*cf.* 533) found that the growth and form of fern prothallia depended upon the quality of the light, red rays permitting an increase in length through cell stretching and blue-violet rays causing shorter forms with more cells. Weston (584) has reported that urediniospores of *Puccinia graminis* failed to produce germ tubes in strong light, but Voorhees (563) has found that diffuse light promoted germination of spores of *Physoderma zea-maydis*.

In a long paper dealing with the "influence morphogenique" of different wave lengths of light, Teodoresco (533) emphasized the need for controlling wave length and energy value of the radiation and the necessity of divorcing the trophic action of food supply from the blastic effects of light. Working with tubers, rhizomes,

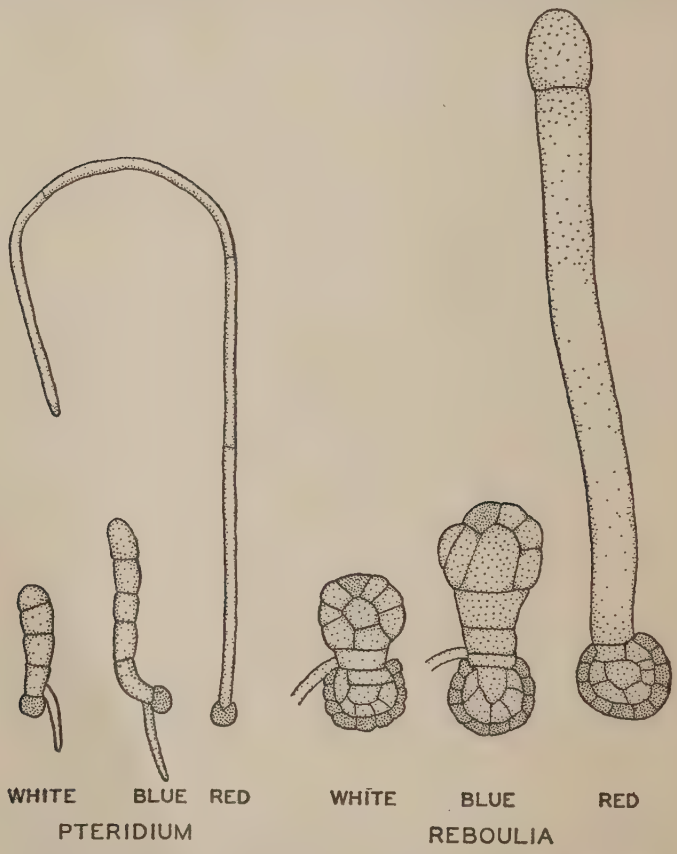

FIGURE d. The formative effect of light upon fern (*Pteridium aquilinum*) and liverwort (*Reboulia hemisphaerica*) sporelings. Plants germinated in white or in blue light are stout and multicellular, while those grown in red light or in darkness tend to become slender and few celled. After Teodoresco (533).

seeds and spores, he was able to show in a convincing manner that darkness and red light permit excessive tissue and cell elongation and that blue light exerts a stunting effect upon growth by keeping the cells smaller. His figures of fern spores germinating in dilute Knop's solution and 1% agar illustrate the striking differences between the very slender few celled filaments under red light or in darkness and the short many celled protonemata which tend soon to broaden out into typical gametophytes in blue or white light. Blue light retards both spore germination and cell elongation. That the tendency for increased cell elongation in darkness is in no way concerned with chlorophyll mechanism is further emphasized by Brefeld's (*cf.* 533) observation of the behavior of the fungus *Pilobolus* whose sporangiophores elongate more in darkness than in light. Results similar to those of Teodoresco have been reported also by Klebs (*cf.* 291) and by Stephan (521) and Hommer (206) for young fern prothallia. Exposure of the germinating spores to red light resulted in a narrow prothallium with a terminal meristem; in the blue light the prothallium became shorter and broader, with a lateral meristem. Gistl (161) observed that the normal form of *Schistostega* protonemata was attained only in the presence of air and light. Schmid (471) found that liverwort spores germinated only in the light. In *Preissia* the cross walls increased in frequency and the cell length decreased with increasing intensity of light. The protonemata of *Lophocolea* and *Chiloscyphus* were single filaments when grown in weak light but became much branched under a strong Osram lamp.

In view of the accumulated facts dealing with the effect of light and darkness upon growth, it seems fairly clear that the linear dimension of organs and their constituent cells tends to be reduced by the incidence of short wave lengths of visible radiation in the blue-violet region of the spectrum. When growth takes place in darkness or in light devoid of the blue-violet rays, polarized growth becomes accentuated. The length of cells in etiolating organs is known to increase manyfold, but little is known concerning the actual changes brought about in the volume of these cells. Recent discoveries concerning the rôle of electric potential and special growth-substances appear to be of great significance in relation to the problem of polarized growth.

Some earlier statements in the literature relative to the axial orientation of germinating eggs of algae in relation to light (392, 589) may be interpreted now on the basis of electrical polarity and differential distribution of formative materials in the cells. Nienburg (354), as well as certain earlier investigators, has reported that light induced polarity in *Fucus* eggs so that the rhizoids grew out from the shaded side. Goebel (163) observed that the radial podetia of the lichen *Cladonia* may become dorsiventral under the influence of one-sided lighting. According to the same author, the young prothallia of *Osmunda* grow transversely to the direction of light, but *Ceratopteris* and *Adiantum* grow toward light at first and later assume a transverse position. The rhizoids of *Osmunda* and *Preissia* are negatively phototropic. Wakeman-Bonne (564) has observed that the spindle during cell division of *Eremosphaera viridis* orients at right angles to the rays of light.

Light growth reaction has been studied in the *Avena* coleoptile by many investigators (101, 577, etc.). Van Dillewijn (101) illuminated coleoptiles by means of three laterally placed mirrors and found that following sudden lighting there appeared a growth depression. Moreover, it was shown that different regions of the coleoptile differ in their responses to light (*cf.* 52, 506). Haig (179) obtained similar information which suggested that two different photochemical systems may be responsible for the differences between the "tip response" and the "base response" in the *Avena* coleoptile (*cf.* 506).

Many fruitful investigations of light growth response of the single celled sporangiophore of the fungus *Phycomyces* have been made in relatively recent years. Tollenaar and Castle (*cf.* 69) have found that when light is suddenly cut off from a light adapted sporangiophore, there occurs a temporary decrease in its growth rate (the "dark-growth response") followed by a gradual return to about the previous rate of growth in the light. Castle (67) has found, further, that when a sporangiophore which is light-adapted and growing at a constant rate is exposed to more intense illumination, a temporary acceleration of growth (the "light-growth" response) is produced, followed by a decrease in rate until the original rate of growth is regained. The reaction time for the light-growth response conformed with the Bunsen-Roscoe law,

provided the time component of stimulating was small, but when exposure was longer than a few seconds, the reaction time to light was determined by the intensity and not by the energy of the flash (70). In general, the sporangiophore reaches a final height which is greater the lower the intensity of light in which it is grown (70). When actively growing sporangiophores, adapted to a series of light intensities covering a wide range, were suddenly darkened and the times required for the onset of the "dark-growth" response (*i.e.,* reaction time) were measured, it was found that the rate of dark adaptation was proportional to the logarithm of the preceding light intensity (69). The kinetics of dark adaptation has been explained as a bimolecular reaction, as are all other photosensory systems which have been examined by different investigators (67). The reaction times of the "dark-growth" response and of the "light-growth" response are compound, consisting of an exposure period and a latent period, this comprising both the true latent period resulting from photochemical action and any "action time" necessary for the response (67, 69).

Development of the fruiting body of at least some mushrooms is dependent upon light, and abnormal forms appear in complete darkness. Boriss (45) has shown that the wave lengths most effective in bringing about normal expansion of the fruit body in *Coprinus* are those between 400–500 mμ, *i.e.,* the same region which is phototropically active. Furthermore, the linear growth rate in cultures of *Sclerotinia* has been found to be greatest in alternating light and darkness than in continuous darkness (180).

To explain the mechanism by which short waves of light exert a depressing effect upon the growth in length of plant axes has not been easy, and only in very recent years have investigators been successful in making an approach toward a satisfactory solution of the problem. The increase in size of the growing vacuolated cell has been regarded primarily as a matter of progressive hydration resulting from the activity of osmotic substances in the protoplast. According to Stiles (525), cells of etiolated plants have been found to possess lower osmotic values than those of normal plants, and intense illumination usually has been associated with increase in osmotic pressure. However, total sugars, nitrogen and ash have been found higher in etiolated shoots of *Berberis*

(479). Hence, the osmotic concentration alone does not easily account for the cell size response to light conditions. Recently, it has been claimed by Montemartini (331) that the shorter wave lengths of light diminish the power of attraction of protoplasm for water. That light brings about increase in permeability of the plasma membrane to various solutes has been claimed by many investigators (*cf.* 53, 528), but Ruhland (449) reported no measurable influence of light upon permeability of beet leaf cells to sugars. Elasticity of cell walls has been found to decrease upon exposure to ultra-violet rays (156). It appears that no final judgment can yet be given concerning the rôle of light in relation to osmotic phenomena and cell size increase.

The study of phototropism, *i.e.,* the growth curvature of an organ in response to unilateral illumination, has made promising advancement toward an understanding of light and growth phenomena. (See (65), (373), and (52) for a discussion of, and many references to the literature of phototropism). By the use of physical methods for measuring intensity of light and response of the plant, Blaauw (31, 32) was able to show a relationship between the energy of the light stimulus and the amount of tropistic response in accordance with the Bunsen-Roscoe law. It was held that light acted by hindering growth and that each part of a plant grew at independent rates according to the amount of light which it received (32). Hence, phototropic curvatures must be due to the difference between the light growth reactions on the two sides of the unilaterally illuminated organ. The inadequateness of this theory as an explanation of light growth phenomena has been brought out by subsequent investigations.

GROWTH-SUBSTANCES

A series of experiments by Boysen-Jensen, Paal, Söding and others (*cf.* 52) led to the idea that there probably exist special substances which regulate growth. In 1928 F. W. Went (577) published the results of important quantitative experiments which confirmed the anticipated existence of a plant growth-hormone controlling the enlargement of the coleoptile of *Avena* seedlings. Furthermore, it was shown that light affected the distribution and activity of the hormone in a definite manner in the plant. Among the many recent papers on the subject, that by Overbeek (374)

affords a good discussion concerning the movement of the growth-substance and its activity in the presence of light in *Raphanus* seedlings. It was found that the production of growth-substance was greatly reduced in the dark but that the response of the *Raphanus* hypocotyl to the hormone was greater in the dark than in the light, the growth response being measured either by total elongation or by growth curvature. The decrease in the ability of the cells to respond to the action of growth-substances (Blaauw effect) is explained, in theory, by the effect of absorbed light quanta upon the electrical charge of intermicellar substance which hold the cellulose pattern in a more rigid position in light than in darkness. (See 5). The hormone was found to move in a polar manner toward the shaded side when the seedlings were unilaterally illuminated so that an unequal distribution of the growth-substance resulted. The effects of different wave lengths of light upon cell enlargement have been investigated indirectly in studies of phototropism, and definite spectrum sensitivity curves have been plotted by various independent workers. In general, the blue-violet has been found to retard growth on the light side of unilaterally illuminated organs much more than the red region (*cf.* 68, 228) of the spectrum. These results of phototropic investigations which deal with localized growth are in general agreement with results obtained when entire plants are subjected to the action of selected wave lengths of radiation.

A discussion of the interesting paper by Thimann and Skoog (536) dealing with functions of the growth-substance in *Vicia faba* may serve to illustrate further the action of light through the growth-hormone. To test the relation of light to the production of growth-substance, comparable seedlings of *Vicia faba* were placed in darkness and in light for four days. At the expiration of this period the terminal buds were removed and tested for the concentration of the hormone by measuring the curvatures produced in *Avena* coleoptiles under standard conditions. Considerably greater amounts of the growth-substance were found in the light exposed plants. Furthermore, a known amount of growth-substance in small agar blocks was placed on the decapitated apex of each of twelve plants, and pure agar without growth-substance was added to twelve other decapitated plants as controls. After four days in the dark it was found that the plants to which growth-substance

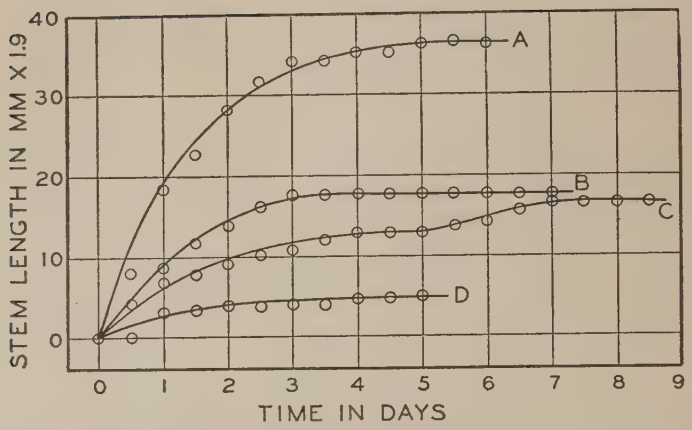

FIGURE e. The formation and action of growth substance in *Vicia faba*. Selected young plants were decapitated and agar blocks with and without growth-substance were applied to their apices. The stem lengths were measured every 12 hours in plants kept in the light and in darkness. Curve "A" represents the rapid growth of plants treated with a known amount of pure growth-substance and kept in complete darkness. The plants of curve "B," having the same quantity of growth-substance added but kept in the light, showed less growth. No growth-substance was added to series "C" which represents growth in the light, nor to "D" which represents growth in darkness. Growth-substance appears to be synthesized in the presence of light (as suggested by the late rise in the growth curve "C"), and exerts its greatest effect in darkness (curve "A"). After Thimann and Skoog (536).

had been added had grown twice as much as the controls. Hence, the growth-substance appears to be made in the light and is capable of powerful action in the dark. Another experiment by Thimann and Skoog was performed as follows: Selected plants were decapitated, all buds and leaves were removed, and the cut surfaces were covered with paraffin. One half of this set of plants was placed in darkness and the other half was kept in the light. Agar blocks, each with 1600 units of pure crystalline growth-substance, were applied to the apices of half the plants in each of the two series in light and darkness, and agar blocks without growth-substance were placed on the others as controls. Every twelve hours the stem lengths were measured. Those plants kept in the light and with growth-substance grew more rapidly than the controls and reached a constant length in 3–4 days. The controls continued to grow steadily and in seven days closely approached the growth

rate of plants with growth-substance. This continued growth increment may be explained as a response to continued synthesis of growth-substance in the stems of plants kept in the light. The controls in the darkened series showed little growth but the plants to which growth-substance in agar blocks had been applied exhibited very great growth. It was concluded that though growth-substance is produced in the light, it functions better in the dark. It may be seen that when plants are brought from the light into darkness, the stored growth-substance acts with greater effect to give a positive dark growth response.

Although the specific and ultimate way in which the plant growth-hormones influence cell enlargement is not definitely known as yet, their discovery in the plant kingdom has created a new approach to the problems of morphogenesis which seems destined to become an exceedingly fruitful field in modern plant science.

GROWTH OF THE PLANT AS A WHOLE

Whether growth of the organism as a whole is considered as irreversible increase in total size or as the transformation of unorganized external material into the organized substance of the entire plant (431), the processes involved appear to be capable of rational interpretation. Biologists, with mathematical inclination, have proposed various and sundry formulae in attempting to express the orderliness of organic growth. Blackman (34) long ago pointed out that the amount of material added in growth is dependent upon the amount already present. He likened the ways of growth to the compound interest law, and stated that the obvious measure of the plant's activity is the rate of interest. This rate of increase (*i.e.,* the efficiency index) which is a result of the growth processes, varies, with the genetic constitution and the environmental circumstances of the individual. By some plants, the elements of the environment are synthesized into living matter at a rapid pace; in others, the rate of assimilation is slow. At any given time the significant rate of growth must be expressed as growth relative to the size of the organism (219). Furthermore, there is considerable evidence to suggest that light influences the course of plant development in other ways than through the supplies of food and moisture.

LIGHT INTENSITY

Using duckweed as illustrative material, Blackman (35) has shown how the growth rate may be accelerated with increasing light intensity up to about 1000 f. c. Above this rather low light value, the rate of frond production is not increased. Many horticultural plants show better growth at higher intensities (*cf.* 597). For example, the tomato gives an increasing gain in dry weight because of photosynthesis proportional to the intensity up to about 4500 f. c. (35, *cf.* 40). That light may have a retarding effect upon the growth rate of certain vegetative organs at the same time, may be seen from Blackman's plot of the increase in leaf area of tomato plants exposed to different intensities up to about 6000 f. c. In unit time, the rate of leaf expansion varies inversely with the intensity of the incident light. In general, it has been found that weeds are able to grow more vigorously and reproduce better under shade conditions than crop plants (597).

Popp grew four different varieties of soy beans under six different light intensities, averaging 4285, 1536, 560, 390, 250 and 25 f. c. in cloth compartments constructed inside a glass house. Weekly measurements of height and general observations of leaf development, thickness of stems, time of flowering, vigor, etc. were made for seven weeks during the course of the experiment. The rate of stem elongation in the initial period of growth varied inversely with the light intensity, while stem thickness was proportional to the intensity. In general, those plants receiving the greatest amount of light were the most vigorous and produced the best leaves and fruit. With decreasing light intensity, there was a gradual decrease in vigor, to the extent that plants grown under 26 f. c. were etiolated and survived only three to four weeks. Using height as a criterion, it was stated that growth of all plants except those under the weakest light "followed the general curve of a monomolecular autocatalytic reaction." The more active phase of the growth curves appeared to be associated with the development of nutritional independence brought about by the ascendancy of photosynthesis, while the later decrease in growth rate appeared to be caused by development of flowers and fruit. This is in accord with the fact pointed out by Murneek (344).

Bolas (40) performed some instructive experiments to determine the influence of light and temperature on the assimiliation

rate of seedling tomato plants. The relative increase in dry weight of young tomato plants during seven hour periods was determined over the temperature range 45–90° F. for each of four different intensities of light—100, 200, 600, and 1000 f. c. At the low intensity of 100 f. c., which might be found in a greenhouse on a dull winter day, the assimiliation rate rose with temperature from 45° F. to about 62° F., but above this temperature the rate fell off and higher temperatures were harmful to the plants. At 600 f. c., representing a bright spring day, the maximum rate of assimilation occurred at 75° F., and on a bright day with 1000 f. c. intensity, a temperature of 90° F. was not excessive from the point of view of assimilation rate. Assimiliation rates were plotted also for each of three different temperatures, 60°, 75° and 85° F., over a range of intensity up to 1000 f. c. At 60° F. maximum assimilation occurred at about 200 f. c. and then decreased considerably with greater illumination. At 75° F. maximum assimilation was at about 750 f. c., the rate falling off toward 1000 f. c. and at 85° F. the greatest assimilation was afforded by the higher intensities in the region of about 1000 f. c. Emphasis was given to the fact that practically all energy required by the green plant for synthesis of organic materials out of CO_2, H_2O and inorganic salts, must be obtained by light absorption. For a given leaf area with a certain chlorophyll content (*cf.* 128) there appears to be a maximum assimiliation rate for any particular light intensity, and for each intensity there is only one temperature at which the assimilatory mechanism of the plant works most efficiently.

Davis and Hoagland (95) grew wheat plants in controlled environmental conditions with various intensities of light and with different daily exposure times. When the yields were computed it was found that tissue formation is more efficient when the radiant energy is distributed at a moderate intensity over a longer time than under the opposite conditions of high intensity and short duration. For any given illumination value there exists a critical temperature, because of the effect of temperature on the rate of CO_2 reduction in the light and the rate of oxidation of the organic materials in both light and darkness. Harvey (188) found that potato and tomato grew well under artificial electric light at 380 lumens per square foot. They were taller than usual at this intensity, but gave a more normal appearance at 680 lumens.

Ashby (14) found that growth of *Lemna* increased with intensity up to 700 f. c. and decreased at 1400 f. c. due partly to a decrease in the amount of chlorophyll and partly to some other process. Under intensities of 350, 700 and 1400 f. c., most rapid growth occurred in continuous light and least in the six hour daily light period. Miss Hicks (201) found that the frond number in *Lemna* colonies grown in the range 15° to 30° C. and under 350 to 1400 f. c. increased exponentially for the period of the experiments. Between 15° and 22.5° C. the increase in relative growth rate with temperature was independent of the light intensity, but at higher temperatures growth varied definitely with light intensity which was probably a limiting factor here. The real rate of carbon assimilation in *Lemna* appeared to be about six times the respiration rate at 25° C. Within the range of exponential growth, the final frond area was independent of light intensity, but the frond weight increased with light.

Ashby and Oxley (16) have made an anlysis of the influence of light intensity and temperature on rates of assimilation and of frond multiplication in *Lemna*. The increase in rate of frond multiplication with light intensity was significant up to about 750 f. c., but the net assimilation rate, calculated on a basis of the increment in dry weight, increased linearly with light intensity over the whole range examined. The effect of light was brought about apparently through some other process than assimilation. It was found that a wide range of multiplication rates could occur at any one assimilation rate, and that frond area was independent of temperatures above 24° C. and of light above 350 f. c. The total area of a colony was found to depend upon temperature and light only in so far as these factors determined the rate at which new primordia were formed.

Steinbauer (519) grew seedlings of *Fraxinus pennsylvanicum* under low light intensities with controlled temperature and humidity, and varied the concentration of nutrients to test the effect of nutrient supply upon the length of the period of survival at subnormal intensities. A greater response to an increase in nutrients was found at higher intensities, indicating greater synthesis, but the minimum light requirement could not be lowered by increasing the amount of available nutrients. Shirley (491), Bates (21) and others have studied the effect of light intensity upon growth

of coniferous seedlings for which light is an important ecological factor. The rôle of light in plant succession has been explained on the basis of intensity as a factor limiting increase in dry weight. In general, those species whose light requirement for survival is comparatively little are able to exist for a long time in the shade, and when favorable light conditions are presented, these tolerant seedlings, already well established, are in a position to replace their intolerant competitors (492).

Clements and Long (81) grew sunflower in a series of varying soil moisture (holard—13, 18, 26, 35 per cent) and for each holard the following light intensities were employed—8, 16, 32 and 100 per cent of normal sunlight. It was found that water assumes the major rôle in stem elongation, and light the larger part in production of dry matter. Shirley (490) investigated the influence of light intensity upon growth of buckwheat, sunflower, tomato, tobacco, California redwood, loblolly pine, etc. The plants were grown in soil under a series of different intensities of sunlight varied by using cloth shades, and with temperature and humidity controlled within limits. Determinations of the dry matter, growth in height, chlorophyll, leaf area, etc., were made. The light requirement for survival of these plants was very low, being less than 40 f. c. for all except sunflower which required a much higher intensity. At low light intensities the dry weight production was almost directly proportional to the intensity up to about 20% of full summer sunlight, but at higher intensities the curve sloped off. Percentage of dry matter in the tops, ratio of dry weight of the roots to dry weight of the shoots, vigor of growth, strength of stem and leaf thickness all increased with increasing light intensity. Above 50% intensity the amount of growth increased very little with further increase in light, which agrees with results of most other investigators (401, 597). The sunflower was able to use light for increment in dry matter up to the highest intensities used, but *Geum* and hog peanut showed a decided decrease in efficiency at the greater intensities. According to Lundegardh (291), the assimilation rate of shade plants, such as *Oxalis,* shows a marked decrease in efficiency at about 1/10 full sunlight, while in typical sun plants, such as *Nasturtium,* the assimilation rate increases with light over a much greater intensity range. Over a range of light intensity, all assimilation curves rise more rapidly at lower intensi-

ties than at higher, the particular form of the curve being dependent upon the kind of plant and other operative factors. Lundegardh (291) has stated that the effect of unit increase of light intensity upon assimilation is greater, the nearer light approaches to a "minimum factor."

LIGHT DURATION

Some effects of varying daily light period upon growth and maturation of plants were known even in the times of John Ray (1686) and Linnaeus (1732), according to Laurie (266) and Smith (504). Since the discovery of photoperiodism in recent years, a vast amount of research has been done in an attempt to formulate the principles of growth and development in relation to duration of light. In 1920 Garner and Allard (145) published the results of their experiments in growing many kinds of plants under various lengths of daily illumination. The action of the light period in initiating or suppressing sexual reproduction in various flowering plants indicated that some plants are more sensitive than others to the length of day factor. In the more senstive group, some are caused to flower more quickly in long days, others in short days. To test a plant for its photoperiodic type, one needs only to grow it under daily exposures of ten hours and eighteen hours per diem, and observe under which, if any, daily light period flower formation is accelerated. Quoting from Garner (144): "When exposed to a day length in excess of the critical, there is in the short-day type pronounced long continued elongation of the stem without flowering; while exposure to a day length shorter than the critical quickly initiates reproductive activity. On the other hand, in the long-day plant, exposure to a length of day in excess of the critical results in elongation of the axis, which is promptly followed by flowering, while exposure to a length of day below the critical tends to limit development to a leaf-rosette stage."

Both types of plants were grown by Garner and Allard (148) under short alternations of light and darkness, extending down to those as short as 5 seconds. In all the plants used, as the alternations of light and darkness were progressively shortened, increasing evidences of chlorosis, impaired nutrition and decreased growth culminated in alternations of about one minute, but with shorter

alternations of 15 and 5 seconds there was a pronounced improvement in the nutrition and growth of the plants. "Increase of the light interval to twice the interval of darkness in each of the cycles had the effect of improving the general appearance and in some cases seemed largely to overcome the retarding action of these alternations on growth" (149). These growth responses to short alternations of light and darkness are the more interesting in view of increased photosynthetic efficiency under conditions of rapid flashes of light which has been obtained in experiments by Emerson and Arnold (119). It is not impossible that these effects of "flashing" light on growth are merely outward manifestations of internal photochemical effects upon specific growth-substances.

Lubimenko and Szeglova (285, 286) have given considerable attention to photoperiodic adaptation and growth as measured by the increase in dry matter per hour of illumination. Maximum utilization of light for growth was attained at a shorter daily exposure than was useful for maximum production of dry substance by photosynthesis. The physiological distinction between short- and long-day plants was ascribed to differences in the enzymatic, apparatus of the cells concerned in the processes of oxidation (respiration) and reduction (assimilation).

Arthur, Guthrie and Newell (12) carried out an elaborate series of experiments with many kinds of plants grown under artificial climates at the Boyce Thompson Institute, where light and CO_2 supply could be controlled on a large scale. Cabbage plants were found to increase in total weight and in carbohydrate content with length of day up to 17 or 19 hours. Clover, soy bean and cucumber increased in carbohydrates and weight per plant with additional CO_2 and supplementary light supplied at night by a battery of 1000 watt lamps. Potatoes grew well on long days but formed tubers under continuous illumination only at comparatively low temperatures (68° F.). Barley and spring wheat, in contrast to potatoes, grew and yielded well at a high temperature (78° F.) when given additional light and CO_2. The weight per plant of barley was found to increase with day length up to 19 hours per diem. Roses, sweet peas, snapdragons, petunias and nasturtiums grew and flowered well with additional light, but geranium, coleus and tomato were greatly injured by continuous artificial illumination. Good growth of tomatoes has since been reported under

outdoor conditions in Alaska where the sunlight effective for growth was practically continuous (92).

Pfeiffer (390) reported that when buckwheat was grown in 5, 7, 12, 17, 19 and 24 hours of artificial light daily, a maximum height and stem diameter was obtained in the 17 hour day. Smith (504) found that maximum growth, expressed as dry weight per day per unit of light, occurred in continuous light for young plants, but as the plants aged the maximum was displaced toward the shorter day lengths. Adams (1, 2) found that plants exposed longest to the action of light generally gave the greatest average weight and height. In the case of tomato, soy bean, buckwheat and hemp, there appeared to be an upper limit of light duration above which no additional growth was made. Cotton has been found to increase its height with increasing day length up to continuous illumination under the experimental conditions which were employed by Berkley (26).

The relation of light to growth vigor is of interest in view of certain recent investigations of heterosis in plants, where the F_1 hybrids show similar efficiency indices but exhibit different degrees of vegetative vigor (15). Malinowski (301) investigated the effect of photoperiods upon hybrid vigor in *Phaseolus vulgaris*. Two distinct strains were crossed and the hybrids grown under long and under short daily light exposures. In long days the F_1 plants exceeded the parents in height, number and length of internodes and size of leaves. In 8-hour days the F_1 plants were reduced to approximately the parental size and flowerng occurred six weeks earlier than in the long day condition. It would be highly instructive to know the effects of light duration upon the efficiency index for growth in plants such as these.

LIGHT QUALITY

The visible spectrum has been shown to exert marked effects upon growth through carbohydrate synthesis and through a special formative action not fully understood, while the infra-red region appears to be active mainly through its temperature effects. The great bulk of literature dealing with effects of ultra-violet radiation upon plants has been reviewed recently by Popp and Brown (402). It seems clear that the short wave ultra-violet from 289–200 micro μ is distinctly harmful, the degree of injury depending upon the

intensity, the wave length and the amount absorbed by the vital tissues (*cf.* 317, 402, 7, 136, 137). This lethal radiation given off by the sun is filtered out by the ozone in the outer layers of the atmosphere, and hence never reaches the earth. Perhaps it is not surprising that artificially produced wave lengths shorter than ordinary sunlight should bring about unusual effects upon organisms which have become adapted to the natural light environment of which these lethal rays form no part. Popp and Brown (402), after a critical survey of the botanical literature, state that even in very slight doses the short wave ultraviolet has never been demonstrated to be beneficial, and evidence from the most accurately controlled experiments to date shows little, if any, beneficial effect of that region of the ultra-violet present in sunlight.

The action of different portions of the visible spectrum upon size and form of plants has received attention from many investigators. Popp (401) grew a number of different species in colored glass houses using filtered sunlight as the source of energy. Very little difference was noted between plants grown under full sunlight and those grown in the absence of ultra-violet radiation. When the blue end of the spectrum, including all wave lengths shorter than 529 micro μ, was excluded, growth was poor, the plants were weak and there was a decrease in fresh and dry weight and an increase in the moisture content resembling the symptoms associated with etiolation. Unfortunately, the intensities were not balanced in the different houses but the data indicate that the blue-violet end of the spectrum is indispensable for normal vigorous growth of plants. Somewhat similar experiments by Shirley (490) have indicated that the blue-violet part of the solar spectrum is more efficient in dry weight production than the red end, when the intensities are 10 per cent of the outside sunlight. Pfeiffer (390) reported better development, as expressed by greater stem thickness, height, leaf thickness, etc., in the full solar spectrum than in any fraction of it. Roodenburg (444) found in his experiments with light from neon and mercury arcs, that the blue end of the spectrum tended to make plants grow stocky. Shirley (490) grew plants in five different colored glass houses with three different intensities controlled by cloth shades in each house. The complete solar spectrum was considered more efficient for the production of dry matter per unit of light intensity than any portion of it.

A further report by Arthur (8) showed that without blue light, plant stems were thin and weak and the leaves small and rolled. When grown without red light, the plants possessed a normal appearance, but growth in height was subnormal due to the low intensity of energy available under the filter glass. Later investigations by Arthur and Steward (11) have suggested that a relatively high proportion of infra-red in the incident radiation may bring about increased elongation of the stems, accompanied by decreased expansion and diminished chlorophyll content of the leaves of buckwheat plants. It was concluded that the efficiency of various gaseous discharge lamps and Mazda lamps in the production of dry plant matter was not related to their emission spectra and the absorption bands of chlorophyll.

Experiments dealing with the influence of near infra-red radiation on plant growth and coloration have been described by Johnston (227) who has pointed out the need for taking into consideration the presence of infra-red energy in order to properly evaluate the effects of the visible region. Marglobe tomato plants were grown under two different distributions of radiation of equal visual intensity, one limited entirely to visible radiation, the other including a large amount of near infra-red energy. After two weeks, the plants exposed to visible plus infra-red radiation were characterized by longer internodes, larger leaves and decreased chlorophyll. These results are in accord with those reported by Stephan (520) who found that *Marchantia* grew abnormally in a light environment with a very high proportion of infra-red rays. However, Forster (132) reported no influence of infra-red rays upon the development of *Marchantia*. Apparently, normal growth of the tomato plant can be obtained under artificial light conditions where the infra-red is eliminated, provided the intensity of visible light is sufficient. It is possible that the difficulty experienced by Arthur (12) in growing tomato plants under long days with artificial light may have been due to the excessive proportion of infra-red.

As a result of the vast amount of accumulated knowledge concerning the radiant energy requirements for successful growth of economic crops, definite recommendations have been made recently for the practice of electric horticulture by Oden (368, 369), Roodenburg (444), Laurie (267) and others. For forcing cuttings and

seedlings in early stages of growth, about .003–.015 g. calories per cm^2 per minute within the wave length limits of .4–1 micron is suggested by Oden (369) as being efficacious. The intensive cultivation of vegetables during winter required from .06–.12 g. calories per cm^2 and the growth of sweet peas, beans, cucumbers, etc., need about 45 g. calories per cm^2 day. Roodenburg (444) recommends, for supplementing daylight, the use of neon low voltage tubes which emit a red light of wave lengths absorbed by chlorophyll and therefore efficient in photosynthesis.

DIFFERENTIATION

Differentiation, in contrast with growth, may be viewed as a developing process whereby are obtained the forms and structures characteristic of different kinds of cells, tissues, organs and species. It seems clear that the morphological aspects of differentiation actually rest upon the different chemical stuffs and physical states within the cells of the organ or plant as it gradually passes from its beginning to its maturity. However, since the fate of a particular part of an individual may be determined by its relative position in the organism, or by chemical changes which may occur in some other totally different (but correlated) part, the organism as a whole must be considered. Differentiation may be regarded, therefore, as the sum of the physical and chemical changes which occur in the maturing organism and the diversified morphological expressions which arise as the result of these conditions.

Loomis (281) has discussed the "growth/differentiation balance" from the chemical point of view, namely, that growth depends on available water and the various elements needed for synthesis of protoplasm, while differentiation is conditioned mainly by carbohydrates. If growth is checked by some means (*e.g.,* by reduction in water or nutrient supply to the top) which does not impair photosynthesis, then the carbohydrates formerly used in protoplasmic synthesis accumulate and serve as raw materials for differentiation. Since the light régime is known to have profound influence upon physiological processes, such as photosynthesis, growth-substance formation and activity, pigmentation, etc., in growing plants, it should be expected also to have marked effects upon the production of their characteristic form and structure, *i.e.,* upon morphogenesis and histogenesis. Furthermore, it ap-

pears highly probable, in the light of modern investigations, that light exerts its influence in the development of plants in many ways which are yet imperfectly understood.

THE PLANT AXIS

An interesting aspect of the formative effect of light upon higher plants is that concerning the shoot/root ratio or the growth and development of the above-ground portion of the plant relative to that below the soil. Garner and Allard (146) found that distribution of food and intensity of growth in the shoot and root of many plants is governed to a considerable extent by the length of the daily exposure to light. Formation of bulbs, tubers and thickened roots, in those species where inheritance permitted, was enhanced by a length of day different from that favorable to vegetative increase. In soy bean, as the length of day was shortened below the optimum for stature or flowering, tuberization occurred. Potato showed vigorous vegetative shoot growth in an 18-hour day but a great proportionate increase in tuber formation occurred in a 10-hour day. The tropical yam, *Dioscorea alata,* under a 12-hour day yielded large tubers, but in a full summer length of day in high latitudes only small tubers were formed. Formation of bulbs was found to be increased as a result of a lengthened daily light period above the optimum for stem growth. For example, the onion produced good bulbs in long days and poor ones in a 10-hour day where the food was used for growth of the tops. Biloxi soy bean in short winter months failed to show top growth but the root system increased in the greenhouse. Maximov and others (308) observed that plants grown in shade have less extensive root systems and a greater per cent of dry weight. Simon (498) reported that shade or darkness delayed or prevented development of the plumule, stem and branches of *Bruguiera eriopetala* (Mangrove) seedlings but had no effect upon the root system. Dahlia cuttings grown in a short day yielded markedly thickened underground parts but in long day conditions there was but little storage of foods in the fibrous root system (598). Many tropical tuber-forming species of *Solanum, Ullucus tuberosus, Oxalis tuberosa* and *Tropaeolum tuberosum* were grown in different day lengths by Rasumov (424). Onions have been found to form bulbs in relatively long days (310). All species attained maximum vegetative de-

velopment and usually flowered abundantly in a long day, while the greatest production of tubers was afforded in short days. The greatest yield of tubers was nearly always produced by pre-treatment with a long day period followed by a short-day period. In several species, short days in the early history of the plants followed by long days in the latter period of development caused reversion of the tubers to stolons and an accompanying increase in vegetative shoots. Similar observations have been recorded by Tincker and Darbishire (543) and Hackbarth (178) for tuberous plants, and by Nightingale (359), Ulvin (553) and Eaton (110) for other plants. The ratio of tuber weight/top weight in potatoes has been found to range from 0.4 in continuous light to 2.0 in short days (106). Werner (583) found carbohydrate accumulation and good tuber formation when potatoes were grown under the following circumstances: when nitrogen assimilation was checked, at relatively low temperatures, under conditions of potassium deficiency, and in short days. Maximum tuberization occurred in medium days, at low temperatures and with nitrogen available. Furthermore, it has been found in general that plants which have grown under light conditions favorable to the accumulation of carbohydrate reserves are better able to resist unfavorable circumstances, such as drought and low temperatures (*cf.* 492).

Some investigators have not found differential growth of the shoot relative to the underground portions when plants were grown under varying photoperiods (*cf.* 572). Beets grown in various day lengths from 4 hours upward have been found to produce a maximum yield of leaves and petioles in 10 hours of light per day, with a decreased formation of leaves and an increased development of roots in longer daily exposures (248). Schick (470) observed that reduction in the day length to 12 hours had no morphological influence upon four potato varieties from Germany, but short days resulted in tuberization of three South American varieties, which indicates that photoperiod may have some effect upon the inheritance mechanism of plants which have been accustomed to the daily light régimes at different latitudes of the earth (*cf.* 106). It has been concluded by the majority of those who have found differential photoperiodic effects on axial growth that the accumulation of materials in fleshy underground parts is not due to an increased photosynthetic activity but arises from inability of the plants to use

the carbohydrates in excess of the current consumption for protein synthesis, respiration and cellular differentiation.

The effect of light intensity and duration upon the root/leaf mass ratio in *Raphanus* has been studied by Johansson (226). An increase in root growth was brought about by increasing intensities of light at all daily exposure periods ranging from 6 to 24 hours, but an increase in leaf mass was occasioned by increased light intensities only in the shorter exposures of 6 or 8 hours per diem. When the root weight as per cent of the total plant weight was plotted against day length, an increase was found up to 10 or 12 hours of light per diem, particularly at the higher intensities, but in longer days the relative root weights decreased. The weight of a unit area of leaf surface increased in bright sunlight and in longer days, provided the light was of sufficient intensity. The leaf weight of unit area was considerably increased in those plants grown in light which was filtered through glass. According to Probst (441), diffuse daylight falling upon the shoot portions of *Linum* and *Lepidium* retarded the growth of the shoot and stimulated the root. Direct illumination of the root retarded its growth. In *Sinapis* and other plants, prolonged illumination of the shoot followed by darkening resulted in increased root growth, possibly due to the mere increase in carbohydrates.

That the C/N ratio is closely connected with the proportional development of shoot and root has been demonstrated by many investigators (94, 199, 359, 433, 499) who have observed that relatively greater proportions of carbohydrates favored root formation. The inhibitive action of light in the formation of adventitious roots in *Tradescantia fluminensis* appears to be due to a mechanical hindrance in the hardened cortical tissues through which root initials can break more easily in the absence of light (319). According to Kellerman (234), in no case does the light period best adapted to food storage in bulbs, tubers, etc., coincide with the daylight period best adapted for upward or top growth of the particular plant under consideration. The nature of the regulatory action of light on the internal processes of the plant, other than those which merely determine the quantity of carbohydrate produced, await satisfactory explanation.

Whether the plant forms a leaf rosette or remains short, stocky and branched, or grows tall and slender, may be determined largely

by the quality and quantity of the incident light. A large group of plants is characterized by a pre-flowering period of growth which is limited chiefly to the formation of a leaf rosette, and when these plants are grown under conditions of a relatively short daily light exposure they remain in this stage for a long time without flowering. On the other hand, long days promote an upward shooting of the axis in this type of plant and flowering subsequently takes place. As an illustration, rosette plants of *Oenothera biennis,* when transplanted to a 10-hour day, showed basal branching but in full sunlight only a primary axis developed (146). Similarly, the form of radish plants may be controlled in a striking way by transferring the plants from one day length to another (*cf.* 553) or by varying the temperature (397). The axis in lettuce is known to remain short in short days, while the flowering axis elongates under long day treatment (448).

That elongation of the plant axis need not necessarily be followed by flowering has been shown by Klebs (240) who was able to induce terminal vegetative rosettes on elongated stems of *Sempervivum.* According to Daniel (91), *Allium porrum,* grown in low light intensity, flowered late and formed fasciations and proliferations in the inflorescences, and in some cases bulblets took the place of flowers.

Garner and Allard (146) have pointed out that as the light period becomes progressively less favorable for upward stem growth, the various responses of plants are those frequently associated with relatively dry conditions, *i. e.,* a tendency toward flowering, increased branching, pubescence, abscission and leaf fall, shortening of the stem, tuberization and increased underground development (*cf.* 337). Pobedimova (398) has also called attention to the effect of intense light on the formation of hairy stems in *Stellaria media.*

Chailakhian (72) grew winter wheat and barley in a series of different daily light durations, and found that various degrees of branching occurred, ranging from a flattened low type in plants exposed to a 10-hour day to a tall, compact habit under conditions of continuous light obtained with daylight supplemented by artificial illumination. The effect of day length upon the habit of cereal plants has been studied also by Hurd-Karrer (215), Purvis (223) and others. According to Hurd-Karrer (213), dormant rosette

stages in winter wheat are brought about by short days and this stage never appears with supplementary artificial light in the greenhouse. Also relatively high temperatures (20–23° C.) during the growth period can prevent rosette formation.

GROWTH REGIONS

Formative effects of the light period upon the growth habit in higher plants appears to be exerted through some modification in growth intensity of the various meristematic regions, which results in apical dominance, or branching, etc. It has been found that intense light tends to have a dwarfing influence, while weak light permits tall and spindly growth. Experiments with different wave lengths of light indicate that the shorter waves exert a strong regulatory action which gives plants their normal appearance, while the longer red waves act much like darkness, except, of course, that chlorophyll is developed and carbohydrates are manufactured. Descriptions of these photogenetic phenomena have been given earlier in the discussion.

The branched habit is indicative of a reduced apical dominance, and in the light of the recent contribution by Thimann and Skoog (536), dealing with the inhibitive rôle of auxin upon the growth of lateral buds, it would appear that some modification of hormone activity may be exercised by the light period. That the arrangement of foliar organs on the axis is also capable of modification has been indicated by the change from opposite to alternate phyllotaxy in hemp subjected first to a short day period followed by a long day régime (460). In these experiments, the photogenetic effect is exercised through some action upon the meristems.

According to Chroboczek (79), the growing points of *Beta vulgaris* which were destined to remain in a vegetative condition yielded very different values for the ratios of diameter to height as compared with plants which later developed seed stalks. Using various treatments to break the rest period in potato tubers, Denny (198) found that the very first chemical changes occurred in the region of the growing points.

Just what the nature of the correlative control over growing points in the plant may be, remains to be shown. It is known that the determinative influence of light upon an aerial part may be transmitted to a subterranean portion of the plant, and buds at the

nodes of stolons may be influenced to grow without a rest period and thus form short lateral shoots. When two coordinate branches of a *Cosmos* plant were subjected to different photoperiods, in all cases the vegetative branch, produced in the long day treatment, assumed a dominant influence over the basal portion which continued harmonious growth; the other flowering branch soon ceased growth and declined (146). Eghis (112) has reported that when soy beans were exposed to 10 hours of sunlight daily for 10 days early in life, flowering was hastened even under subsequent conditions of long daily exposures in later life, but only the first axis was capable of this "after effect." The lateral branches which arose later flowered at the same time as did the controls which had never been subjected to short days. Kondo and others (250) exposed the vertical halves of rice plants to short and long days, *i.e.*, one half to 24 hours and the other to 8 hours of light daily, and found that no part of the plant had any influence on the other parts.

However, experiments of Rasumov (425) have indicated the possibility for certain effects of localized photoperiodic stimulation to be readily transmitted morphologically downward but not upward. Our knowledge of the influence of auxins upon bud development and cambial activity (536, 511) lead to the assumption that some kind of organizing stuffs may be concerned in the differential expansion and maturation of the plant body.

TISSUE DIFFERENTIATION

That differentiation of tissues in the plant axis is conditioned by light to a considerable degree has been shown by investigations of etiolation and studies of the anatomy of plants grown under different light conditions. Bonnier (42), an early student of photomorphosis, observed the influence of continuous artificial light upon plant structure and anatomy. MacDougall (294) and Priestley (407, 414) have described the weak vascular and supporting tissues characteristic of etiolated plants, and the latter has shown how structural and morphological changes can be induced by even brief exposures to light. Various twining plants, when deprived of light for a few days, lose their power of circumnutation, due to some other cause than starvation (353, *cf.* 365).

Pfeiffer (390, 391) studied the anatomy of plants grown under different intensities and ranges of wave length. The full solar

spectrum rather than any part thereof yielded better developed tissues, as shown in the diameter and vascular anatomy of the stem, though it was difficult to conclude regarding the effects of radiation of different wave lengths, because the energy values were not equated. Deats (96) found that the amounts of phloem and xylem in stems of tomato and pepper varied directly with length of day. Variations in cell wall thickness and size of epidermal and cork cells varied in a similar manner with the light duration. Reid (437) investigated the effects of light on development of seedlings and reported that carbohydrate synthesis promoted increased cell wall thickening in the xylem and more extensive lignification of the phloem fibers. Penfound (386) observed that the anatomy of *Helianthus* and *Polygonum* grown in full sunlight differed from shade grown plants in that the roots and hypocotyls possessed a greater diameter and greater area of xylem, and more and thicker walled mechanical elements. In the castor bean, the diameter and amount of xylem in the roots, the xylem area and size of the cells and wall thickness in the stem varied directly with the insolation and soil moisture content. Doroshenko (104) reported that flax exposed to a limited day length grew less in stem thickness and showed decreased development of xylem and phloem and increased diameter of the pith.

LEAVES

The form and anatomy of leaves in some plants is affected by light. Bright light produces relatively thick well-differentiated leaves, while leaves growing under reduced illumination are thin and poorly differentiated. According to Lundegardh (291), many plants, such as beech and geranium, have the ability to form typical "shade leaves" in the shade and typical "sun leaves" in the sun, while other plants form only "sun leaves" or only "shade leaves."

The effect of light intensity upon the number and size of the chloroplasts present in leaves has been studied by Lubimenko (*cf.* 307, 411) and by Euler and others (121). Typical sun plants possess smaller chloroplasts than shade plants. Adaptation to shade is shown by reduction in leaf thickness followed by decrease in the number of plastids together with an increase in their individual dimensions and chlorophyll content (411). Geiger (155) described some of the peculiar properties of an extreme shade plant,

Aspidistra elatior, which thrives in habitats furnishing 6–8 per cent of normal sunlight intensity and is capable of surviving without etiolation in 1/200 normal sunlight. The leaves possess 1/10 as many stomata as many sun plants and the intercellular volume is about 19 per cent of that of sun plants. Reed (432) found the number of stomata per mm² in the shaded leaves of *Citrus limonia* (Eureka lemon) reduced to about half the number in the sun leaves of the same tree. Haberlandt (177) has given much attention to the problem of sun and shade leaves in the *Crataegomespili. Cra-*

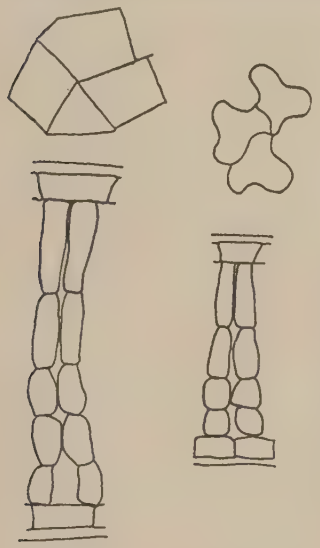

FIGURE f. Variation in the structure of *Crataegus monogyna* leaves grown in direct sunlight and in shade. "Sun" leaves are thicker and possess more palisade tissue than "shade" leaves. Also the side walls of the epidermal cells are straight in leaves which were grown in bright sunshine and curved in leaves which developed in subdued light. After Haberlandt (177).

taegus monogyna is characterized by having straight walled upper epidermal cells and thick leaves with three palisade layers in the sun, and curved epidermal cell walls and thin, less differentiated leaves in the shade. *Mespilus germanica* possesses curved walls in the upper epidermal cells of both sun and shade leaves, but the shade leaves are decidedly thinner and less differentiated. Experiments with *Helianthus* (386) grown in full sunlight and in the shade indicate that with an ample water supply, sun grown plants

possess larger leaves with larger epidermal cells, larger mesophyll and midvein, and more numerous stomata. As Blackman (35) has shown in tomato, the increase in leaf area per unit time may decrease as the light increases, though the dry weight continues to gain. This again suggests that growth regulation is influenced by light through processes other than the synthesis of food materials.

The formative effects of light upon leaves have been described by Priestley (407) and by Ewing and Priestley (413) as a result of their work with the phenomena of etiolation. The outstanding thing about plants grown in absolute darkness is the failure to develop leaf laminae of any appreciable size. Trumpf (550) was able to demonstrate the action of short light exposures in bringing about leaf expansion. Brief exposures to blue or white light when the plants were under chloroform anaesthesia, or at low temperatures (3–4° C.), caused some kind of action which was carried over in the plants so that later under ordinary atmospheric and temperature conditions normal development took place in the dark. Priestley believed that photochemical action on the inert materials in the cells must have taken place under these conditions, and that this unknown substance exerted its influence upon future development.

Li (276) has observed that both formative and extension phases of leaf development in *Ginkgo* require light. For formation of leaf primordia, the light requirement is low, even 2 m. c. sufficing for production of foliar initials. Stronger light is required for the extension phase of leaf growth, and different parts of the blade have different light requirements for expansion. Reid (436) reported that seedlings grown in light in the absence of CO_2 had larger leaves, and cotyledons which weighed more than those of seedlings grown in darkness.

The photogenetic effectiveness of different regions of the spectrum upon form has been studied at length by Teodoresco (533) who observed that blue light hinders petiole elongation and favors growth of the leaf surface. Bizarre filamental forms were noted in liverwort and moss gametophytes grown in red light and darkness but blue or white light induced normality of form. Funke (138) has discussed the results of extensive experiments with *Potamogeton natans, Alisma, Plantago, Sagittaria sagittifolia* and *Sagittaria subulata* which form two sorts of leaves, namely, linear and immersed in their youth, and later, aerial and well differentiated

blades. In red and green light the leaves never develop beyond the linear stage, in blue light the aerial leaves with blades are formed just as they appear in ordinary daylight. When growing plants were exchanged from red to blue, and *vice versa,* an immediate adaptation to the new radiation environment took place. That intensity of light along with the nutrient salt ratio may have some effect upon leaf form in *Potamogeton perfoliatus* has been suggested by Pearsall (384). Popp (401) and Pfeiffer (391) both reported that leaf development was abnormal when growing plants were deprived of the blue end of the solar spectrum. The growth pattern of *Tropaeolum* leaves in normal and reduced illumination has been analyzed mathematically by Smirnov and Zhelochovtsev (502). Variation in the light conditions modified the fundamental field of growth; and ordinary daylight, as compared with shade, stimulated leaf expansion in the early stages of development from the bud. The recent correlation of growth-substance concentration with growth vigor in *Nicotiana* leaves (17) appears to be of considerable significance for the explanation of differential growth patterns which are subject to modifications by the changing environment.

From the standpoint of light duration in relation to leaf development, it has been found that the growth period is longer and the size greater in leaves subjected to relatively long light periods alternating with short periods of darkness than when grown in continuous light (430). Maximov (305) grew plants under artificial light and reported that differentiation of mesophyll and palisade tissues was greater in continuous light than in alternating light and darkness. Ulvin (553) found that radish leaves were thinner in plants grown under continuous light, as compared with those grown in alternating light and darkness. Deats (96) reported the greatest leaf thickness and size in tomato and pepper when grown in relatively long days. However, Pfeiffer (390) observed that thinner leaves were produced in pepper and thicker leaves in tomato grown in long days. These differences of leaf structure observed in various species in response to light conditions may be regarded as the result of the interaction of a number of factors such as the genetic constitution of the plants, the intensity, quality and duration of radiation, and the conditions imposed by soil nutrients and water supply.

The phenomena of abscission and leaf-fall in relation to photoperiod has been investigated by Garner and Allard (146) in *Rhus glabra, Liriodendron tulipifera* and other plants. Several individuals of these species were grown outdoors during the summer and were transferred into the glass house in early autumn, where one lot of plants was given the light of natural day length and the other was given daylight supplemented with artificial light of low intensity in the evening. The lot of *Rhus* plants which were provided only with ordinary daylight dropped their leaves, but the other plants in long-light periods retained their dark green leaves. The *Liriodendron* trees treated with supplementary light also kept their leaves and grew new ones, while the other lot of trees abscissed their leaves and remained dormant. This type of behavior was not characteristic of some other species of plants in the experiments. Kind (236) has observed that in autumn, the leaves of poplar, linden, chestnut, etc., situated near street lights remained green on the trees from two to three weeks longer than usual. Kramer (252) has found that yellow poplar seedlings given supplementary electric light until midnight never became dormant but continued to grow through the winter. These observations appear to be of importance in view of the newer knowledge concerning plant growth-substances which prevent abscission of petioles (*cf.* 581).

REPRODUCTION

The formative influence of the light period upon plants is of great interest in connection with initiation and suppression of sexual reproduction. In 1920 Garner and Allard (145, *cf.* 144) announced that the behavior of plants with respect to development of reproductive stages when grown under different daily light exposures would permit their classification into three groups: (a) the indeterminate type which is not sensitive to the photoperiod over a wide range; (b) the short-day type in which flowering is promoted by relatively short days; and (c) the long-day type in which reproductive processes are favored by long daily periods of exposure to light. The critical light period which may be termed the dividing line between long and short-day plants appears to lie somewhere near 14 hours of light per diem, but in testing the photoperiod type of any plant it is usually a safe procedure to grow the unknown under a decidedly short period of 10 hours and also

under a markedly long period of 18 hours (144). If flowering be materially delayed under the short-day treatment, the plant should be regarded as belonging to the long-day type as, for example, *Avena, Triticum, Raphanus, Rudbeckia,* etc. If the short-day treatment hastens flowering, the plant should be characterized as a short-day type as, for example, *Aster, Cosmos, Nicotiana, Salvia,* etc. In case the time from planting to flowering be substantially the same under the two treatments, the plant may be considered as belonging to the indeterminate group, as in the case of *Fagopyrum.* Since the discovery of photoperiodism, scores of papers have been published on the photoperiodic response of numerous species of plants, including weeds, flowers, cereals and vegetables. According to Moschkov (337), many trees and shrubs also exhibit photoperiodic response. Among woody species, *Poinsettia* and *Bougainvillea* are short-day plants, and *Hibiscus syriacus* is a long-day type (3). The photoperiodic characteristics of numerous kinds of plants have been recorded in tables compiled by Redington (429), Czaja (90) and others. An extended discussion of the detailed data is not possible here.

Garner and Allard (149) found that darkening plants in the middle of the day for periods of 1 to 5 hours generally failed to influence the reproductive activities in any way comparable to the effects obtained by excluding early morning or late afternoon light. The effects of midday darkening were essentially those obtained in long days. Under controlled conditions, series of different plants, including *Cosmos, Delphinium, Rudbeckia,* etc., were exposed to different short alternations of artificial light and darkness ranging from 6 hours to 5 seconds. As a rule, all the alternations were favorable for flowering in the long-day plants, and unfavorable for flowering in the short-day plants. The plants behaved as if they were exposed to a long day or to continuous illumination in so far as flowering was concerned, but very important differential effects were obtained with respect to vegetative growth, as discussed previously. The differences obtained in growth and reproductive responses under the well-controlled conditions of these experiments suggest that of the many reactions which are set up in the plants, certain processes must be affected more than others by the light régime, and in some instances the balance swings in favor of vegetation while in others the final trend is in favor of reproduction.

The significance of the photoperiod in growth and maturation of plants in different regions of the earth has been studied by many workers (286, 309, 427, 542, 543, 310, 594, 122, 470). The results may be summarized as indicating that with increasing latitude, light and temperature conditions become less favorable for flowering in short-day plants, while long-day plants, having a high critical light period, are unable to flower and fruit successfully except at high latitudes. It is believed (145) that annual, biennial and perennial plants are largely expressions of the effect of the prevailing seasonal range in day length, and that the photoperiod is an important factor in the natural distribution of plants (286). Doroshenko and Rasumov (105) reported that many varieties of wheat, barley and beans which have been grown for a long time at higher or lower latitudes possess the characteristics of short- and long-day plants, respectively. It may be that environment (*i.e.*, daily photoperiod) has modified the flowering expression of different races of plants at different latitudes and that these characters have become more or less fixed. Little is known concerning the genetics of the time required for flowering, though Rasmusson (422) has found two main factors in *Pisum* showing partial dominance toward lateness.

Laboratory determinations of the influence of wave lengths, optimum intensity and duration of the light exposure upon plant development have been possible only as a result of the invention of efficient and appropriate mechanical and electrical apparatus in recent years. The experimental technique in light investigations has involved the use of elaborate equipment in many instances where it has seemed desirable to control the temperature and moisture, as well as light conditions (148, 12, 268, 400, 490). Hendricks and Harvey (194) used specially constructed apparatus which permitted growth to maturity under artificial light as the sole source of energy. The range of intensity employed in the different series of experiments was from 50 to 10,632 f. c. For each of the 45 kinds of plants there was reported a certain intensity range, narrow or broad in different instances, in which blooming and seed production took place. Flowering occurred for different plants under continuous illumination in different ranges of intensity (with the temperature maintained between 20–25° C.) as follows: maize 500–3,000 f. c., tobacco 800–10,000 f. c., squash

500–750 f. c. Maximov (305) found that wheat and peas bloomed in continuous light, but flowering was delayed in buckwheat and prevented in soy bean under the conditions of the experiments. Substantial increases in the yield of sweet pea flowers have been obtained with electric light supplementing daylight (190). Adams (2) was able to grow the castor bean from seed to seed under artificial light, and many investigators have obtained increased yields of fruit and several generations of cereal grains in one year by employing artificial light supplementary to daylight (187). McKinney and Sando (313) obtained mature seed from winter wheat in 100 days by growing plants in an 8-hour day at 50–60° F. during the first 54 days followed by $17\frac{1}{2}$–$18\frac{1}{2}$-hour days at about 70° F.

Long ago it was found that flowering plants were not able to form functionally mature stamens and pistils (294) in complete darkness. Recently, Colla (83) has reported that hyacinths with ample food reserve, when exposed to ultra-violet radiation, flowered and shed pollen, while control plants kept in complete darkness failed to flower. Wann (568) observed that fruiting in *Marchantia* was promoted by the use of supplementary weak electric light and Schappelle (465) found that the orange-red region was effective in this respect. Garner and Allard (147) showed that the flowering conditions which were produced in illuminated portions of a plant were able to bring about the flowering effect in other darkened branches of the same plant. The amount of light energy which is required for normal development and formation of functional flowers depends upon the genotype and, furthermore, the effectiveness of light in the formative processes appears to vary considerably during the ontogenetic history of the individual plant (71, 369). Ramaley (417, 418) has reported concerning the influence of ordinary electric light supplemental to daylight upon the flowering of 100 different species of greenhouse plants. The researches of Rasumov (426), Withrow (591), Wenger (576) and others lend support to the earlier findings of Garner and Allard (146) that weak supplementary illumination of approximately one thousandth the intensity of sunlight is effective in promoting flowering response in long-day plants.

Though sunlight is probably a better source of energy for growing plants than artificial sources now available, the use of tung-

sten incandescent lamps and neon discharge tubes has been worked out experimentally with great success in many laboratories (369, 444). Oden (369) and associates have demonstrated the value of supplementary lighting to force seedlings and to enrich the flowering of certain plants. The fundamental principles of electro-horticulture and their applications to the culture of commercial greenhouse crops have been discussed by Greene and others (171) and by Laurie and Chadwick (267). The observations of Oden, with respect to the proportions of different wave length components and the effects upon plant development, are of considerable interest. In *Convallaria,* the proportionate increase in the red light emitted by tungsten lamps operated at reduced voltage favored flowering, while light richer in shorter wave lengths, obtained by operation at a higher voltage, retarded flower development. In forcing, it was claimed that the infra-red spectrum ranges are necessary for normal elongation of the flower stock. Development was most favorably promoted in long-wave radiation in pea, raspberry and string bean, while growth was enriched by short-wave rays in radish, dill and lettuce.

The significance of the quality of light in photoperiodical response has been further elucidated by the extensive experiments of Rasumov (426) using long-day wheat, oats, bean, poppy, *Cicer,* pea and hemp, and short-day millet, maize, soy bean, hemp, potato and Mexican bean. These plants were grown on 10 hours and 17–18 hours of daylight alternating with darkness, and with 10 hours of daylight supplemented by filtered light of six different wave length ranges and controlled intensities. By replacing the dark hours with different wave length bands of equated radiant energy, it was found that the long wave red rays were active in promoting processes of reproduction in both the long- and short-day plants. The shorter wave lengths of the green, blue and violet, when applied separately or together, acted like darkness with respect to initiation of the flowering stage. There was some variation in the quality and intensity of light required by different kinds of plants, but for all the crops investigated, the minimum intensity was very low, *e.g.,* of the order of 10 lux. Since the magnitude of the radiant energy capable of determining the course of differentiation was well below the compensation point, it was assumed that the formative action of light is not exerted indirectly through

photosynthesis of carbohydrates, but directly through some mechanism which regulates the use which the plant makes of its food.

Additional evidence in support of the idea that very low intensities of the longer rays of light are effective in promoting the flowering response has been given by experiments performed by Wenger (576). Aster, a long-day plant, was grown in daylight supplemented with tungsten light over a series of varying intensity for 10 hours each night. Maximum and earliest flowering occurred in all instances where the plants received supplementary illumination of the lowest intensity, *i.e.*, .3 f. c. With increasing intensity, flowering was delayed and reduced in amount, and vegetative growth was increased. Withrow (591) reported experimental results obtained on the flowering responses of pansy, aster and stock grown in the winter daylight supplemented with artificial radiation of controlled intensity and selected wave lengths to maintain an 18-hour day. With supplemental white light even as low as 1 f. c. marked acceleration of flowering production was noted. In the experiments with supplementary blue, green, yellow, orange-red, red, extreme red and infra-red radiation, the most marked responses were produced by radiation in the region 620 to 720 micro μ.

The response of plants to relative length of day may be influenced by temperature and humidity conditions obtaining during the period of growth. Garner and Allard (146) found that lower temperatures tended to conserve the stored energy and delay the time of flowering due, probably, to regulation of the respiratory activity. Gilbert (158) observed in soy beans and cotton that there was retardation of flowering at lower temperatures and higher humidity, while flowering of *Cosmos* was speeded by these same conditions. Formation of flower primordia in *Xanthium* was considerably influenced by temperature, but *Salvia* and buckwheat exhibited no particular response to varied temperature and humidity conditions in the range employed. Adams (2), Bolas (40), Blackman (35) and others have emphasized that temperature must always be taken into consideration in experiments dealing with the rôle of light. Furthermore, it has been demonstrated that the temperature factor may control the vegetation/reproduction balance in a very striking manner in many plants, such as celery, cabbage, beet, etc. (539, 79, 323).

The interrelationship between temperature and photoperiodic stimulus has received considerable attention in Russia where the principles of photoperiodism and jarovization have been found to be of great practical importance in the successful production of economic crops. In 1918 Gassner (151) reported that the length of time required until flower formation in winter wheat decreased with decreasing temperature at germination in the range plus 26° to minus 1° C. In recent years, the conversion of winter plants into spring plants has been accomplished on a large scale either by pre-treatment of germinating seeds in a definite manner (292, 306) or through regulation of daily light exposure during the growth period. Jarovized seeds differ from ordinary unjarovized seeds in that, other factors being equal, the former develop into ordinary spring plants and mature within one season. Chialakhian (72) exposed barley, wheat, etc. to different light régimes and found that long days favored the maturation of grain in the fall of the same season (*cf.* 313). Purvis (416) reported that the germination temperature, as well as the photoperiod, influences the growth and maturation of winter rye. Winter rye, germinated at 1° C., behaved as a long-day plant, but when germinated at 18° C. it responded like a short-day plant in that differentiation of flower initials proceeded more rapidly in short days. If differentiation of flower primordia is accepted as the basis of classification of photoperiodic types, then the spring cereals are true long-day plants. The winter varieties germinated at high temperatures are short-day plants with respect to flower initiation but demand long days for subsequent maturation, while the winter varieties germinated at low temperatures are similar to spring varieties, *i.e.*, they behave as long-day plants. Gilbert (157) grew cocklebur plants in long and short days and under conditions of high and low temperature for each photoperiod. When subjected to high temperatures, flowering occurred in the short day treatment in two weeks and under long day conditions in seven weeks, but in a low temperature environment the vegetative period was prolonged in short days to 16 weeks and in long days to 13 weeks.

SEX REVERSAL AND REJUVENATION

Variations in light appear to be capable of bringing about a shift in the physiological trend of some plants to the extent of

causing such marked phenomena as rejuvenescence, sex reversal, etc. Vegetative growth of a plant frequently terminates with formation of fruits which are believed to divert the available nitrogen away from the vegetative growing points (345). Sande-Bakhuyzen (454) has shown that the water content of vegetative organs of wheat decreases rapidly at the time of fruit formation, and exhaustion and death of all parts except the fruits finally take place. Murneek (343) considered gametic union to be the cause of localized metabolic gradients which exert a detrimental influence upon the other metabolically weaker parts of the plant. In whatever manner senescence is hastened through the accomplishment of reproduction, it seems clear that light periods which are not favorable for flower production ought to defer the arrival of old age. The youthful activity of the vegetative meristems can be prolonged by appropriate light periods (146) and by relatively high temperature conditions (79). Klebs (240) was able to control vegetation and reproduction by manipulating the light and inorganic nutrients. Garner and Allard (146) reported rejuvenated vegetative activity after flowering by manipulating the photoperiod in appropriate ways for soy bean, wild aster, *Poinsettia* and other plants. Schaffner (460) reported three such rejuvenations in individual hemp plants wherein flowering was induced by short days alternating with a period of vegetative development under artificially controlled long day conditions.

Since control of vegetation and flowering can be exercised by light, it is not surprising that sexual expression fluctuates with variations in the photoperiod. Photoperiodic modification of the processes of vegetation and reproduction in maize is well known (112, 117). Eghis (112) grew a race of maize under 12 hours of daily light and obtained complete reversal of the staminate flowers to the functional carpellate condition, so that ears developed in place of tassels. Also, Schaffner (461, 462) has reported that the male flowers in maize may be suppressed completely by decreasing the light period to a suitable day length. Furthermore, the same author (463) has shown that staminate hemp may undergo sex-reversal and develop carpellate flowers when grown in the short winter days of a north temperate latitude. McPhee (314) has found that the time of flowering of hemp is controlled largely by the relative length of day and night, a seven

hour period of daylight accelerating flower formation to an optimum extent. Furthermore, more intersex types were formed in the winter months. Tiedjens (540) reported an increase in the number of staminate flowers in cucumber grown in abundant light, and an increase in pistillate flowers under reduced light conditions. Gardner (143) found that low carbohydrate supply in strawberry at the time of flower bud differentiation led to a failure of female flowers in a variety which is normally hermaphroditic. If sexual expression may be assumed to result from differential rates of activation of the genetic factors for male- and femaleness (*cf.* 28, 84, 165), then it is no more difficult to account for variations in sex than to explain the shifts in the growth/differentiation balance or any other phenomenon intimately associated with the course of metabolism.

The relation of light to fruit development has been shown to be of great importance through the hastening or, in other instances, through the repressing effect upon flower formation. That a more direct relation may exist has been indicated by Gray (170) who found that, though a moderate reduction in intensity was without effect upon the set of fruit in sour cherry, heavy shading with burlap caused abortion of the embryos. In order to explain the behavior of the fertilized ovary as a growth center, the suggestion has been made that hormones may be concerned in the establishment of a metabolic gradient (*cf.* 311, 345). Too few facts are known as yet to permit the formulation of a sound physiological explanation for the morphologically well known story of reproduction.

DIFFERENTIATION OF THE PLANT AS A WHOLE

Recent studies of the differentiation of growing organisms have led to the suggestion that the morphological plan of the individual is determined by a basic chemical ground plan of growth which is capable of modification within wide limits in space-time (350). According to the scheme of Huxley (219), the processes involved in growth and differentiation in plants may be classified into three phases: (1) chemo-differentiation, which includes invisible determination of the specific fates of different regions of the embryo or generating part through orientation of the chemical pattern; (2) histo-differentiation, which embraces tissue differentiation,

and the assumption of the definitive general form-plan; (3) auxano-differentiation, which consists of the subsequent quantitative growth changes.

The action of light as a stimulus causing living plant cells "to adopt appropriate rôles from a limited repertoire" (*cf.* 537) according to the genotype, has been discussed already at considerable length. That photochemical reactions take place in plants is well known from extensive investigations concerning chlorophyll and photosynthesis of carbohydrates (283, 119, 570, 19), the formation of anthocyanin pigments (9, 370), the movements of stomata (459) and the effect of light upon the synthesis of plant growth-hormones (17, 347, 536). Further indirect evidence comes from the great volume of literature dealing with phototropic response to specific wave lengths of radiation (*cf.* 65), the formative influence of brief light exposures upon etiolated plants (407, 437, 550) and the collective data concerning the development of plants grown under controlled intensity, wave length and duration of radiation (12, 146, 194, 426, etc). Also certain physical effects of light are known in the modification of normal polarity by photoelectric potential (47, 162, 489, 565, 566), and in the regulation of water requirements through transpiration (13); also in other ways, as suggested by light growth reactions (65, 70) whose specific mechanisms have not yet been fully explained. On the assumption that metabolic and structural differences between species are causally related to specific differences in chemical constitution, the question naturally arises as to how the various morphological characters of form, size and structure are attained in a correlated fashion. How does light determine the final swing of the balance of processes in a given direction which results in the successive initiation of vegetative organs, the formation of flower initials, the determination of sex, or the rejuvenescence of the aging individual? The answer does not yet appear simple. Histo-differentiation is obviously at work in the first formation of the organ-rudiments destined to become root, branch, leaf, flower or fruit. It has been stated that, in general, the younger the tissue, the lower the C/N ratio (200), but regulation of the proportionate amount of carbohydrates in the plant through light action and by other means has not been found capable of explaining organ differentiation. The available evidence from many dif-

ferent sources suggests that light influences the chemical (146, 199, 244, 536), and physical (79) conditions which are of the utmost significance for the initiation of organ primordia as well as for the maturation of the differentiating tissues, but the exact nature of the processes which accomplish these results is not known.

After organs have been initiated by the interaction between genetic factors and environmental stimuli, or in whatever specific manner, their subsequent development takes place in an orderly fashion according to the well known laws of differential growth. Huxley (219) has shown clearly by numerous examples in animals that over a considerable range of auxano-differentiation, the relative growth rate of the organ to the relative growth rate of the body remains constant. That the constant differential growth ratio between different parts of a plant may be influenced by light has been demonstrated (219, 383). For example, the differential growth of shoot weight compared with root weight in normal and etiolated seedlings of *Pisum sativum* yielded values for the differential growth ratio (k) ranging from .90 to 1.15 in the light and 1.75 to 2.65 in the dark. This simply means that the shoot grew more rapidly than the root in the etiolated plants, while the shoot and root grew at approximately the same rate in the normal plants. It has been shown in many instances that growth vigor in different organs of a plant can be modified greatly by variation of the photoperiod (135, 508) and that with proper adjustment of the day length the rate of vertical elongation and final stature may be increased or decreased over a very great range.

Certain aspects of the light influence in morphogenesis may be explained in part, on the basis of specific substances (hormones) and their distribution due to normally occurring electric potentials (162, 246, 419, 565, 579). As an example, there may be mentioned the production of plant growth-hormones in buds, leaves, (17, 510) etc., and their distribution in a polar manner to other portions of the plant body where effects are brought to bear on the processes of growth and development. In other instances, the effect of light upon the organization of the plant as a whole may be carried out through a somewhat different mechanism. Harper (186) observed that in the myxomycete *Polysphondylium,* normal alternation of day and night favored the production of more and

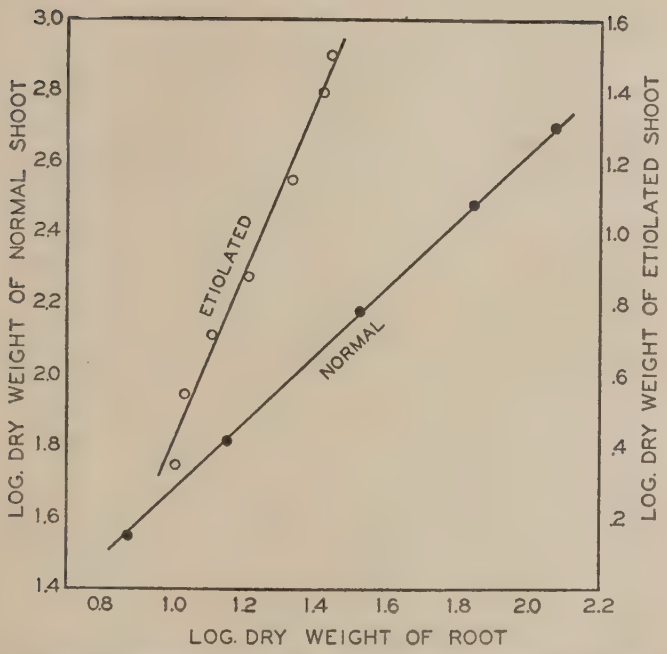

FIGURE g. Constant differential increments in the dry weight of the shoot and the root of the garden pea (*Pisum sativum*). The young plants were germinated and grown in nutrient solution. The etiolated plants were kept in darkness, and the normal plants were exposed to ordinary daylight and darkness. Note how the dry weight of the shoot in the etiolated plants increased with relatively great rapidity. Data from Pearsall (383).

smaller plants, while almost continuous darkness brought about the production of larger and fewer plants. These observations were interpreted as "indicating that cell growth and division go on equally well under both sets of conditions, but that the processes of aggregation and integration tend probably in darkness to favor the gathering of the myxamoebae from larger areas to the points of integration, thus resulting in the formation of fewer and larger plants per unit culture." It appears that modification and development of the form of cells, organs and organisms may or may not occur simultaneously with growth. From this viewpoint, the cells of a multicellular organism are considered as behaving more or

less independently in growth and differentiation and their integration into characteristic multicellular tissues, organs and organisms is a matter of their physical and chemical interrelationships.

It has been shown how light affects the physical and chemical constitution of plants. The light synthesis of food materials and "organizing" substances, and some degree of light control over their activity in the processes of integration and correlation of the whole organism has an important significance for morphogenesis. It is relatively easy to understand how light can bring about a quantitative effect upon such characters as gross size and form, and even upon microscopic shape and structure of cells which comprise the tissues of the plant, when the organism as a whole is structurally considered as the sum total of all its parts. Size and form in the plant depends upon the number, size and form of the constituent cells, and the characteristics of these individual cells depend upon the nature of the molecular pattern of which they are comprised. This is almost as far as it has been possible to carry the story, but it is not quite the end. It has been shown, further, that the quanta of light rays which are absorbed by the atoms of matter become activated so that photochemical reactions ensue, changes in temperature occur and photoelectric potentials are developed. Photomorphosis (the configuration brought about by light) in plants would appear to rest upon both qualitative and quantitative aspects of the physico-chemical situation. The synthesis of special compounds in photo-chemical reactions, the differential catalysis of physiological processes, and the correlation of the whole plant by electrical potential and other interchanges, such as may be conditioned by surface tension, protoplasmic streaming, etc., suggest a variety of possible ways by which light may contribute to growth and differentiation of the plant body. As Dixon (102) has written, "a long chain of energy and of material transformations, imperfectly ascertained and understood, usually intervenes in biological phenomena between what we recognize as the cause and the result." From the line of reasoning developed in this review of the literature, it may be concluded that the relation of light to the structure and pattern of plants depends upon its quantum action in the minute electrical structure and pattern of matter. The many gaps in the record, due to the complexity of the material and of the processes, remain for future investigators to complete.

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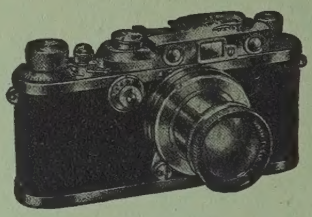

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